LAKE MICHIGAN MASS BALANCE STUDY

PROGRESS REPORT

DIETS OF FORAGE FISH IN LAKE MICHIGAN

by

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METHODS

Forage fish and zooplankton were sampled in efforts to determine spatial and temporal effects on diets of forage fish in Lake Michigan. Collections were made off of three ports (Sturgeon Bay, Port Washington, and Saugatuck) which provided a north-south gradient within Lake Michigan. Sites at Sturgeon Bay and Saugatuck were relatively near-shore; whereas the site off Port Washington was located closer to mid-lake. Three seasons (spring, summer, and fall) were sampled in 1994 and two seasons (spring and fall) in 1995. Five species of forage fish were collected; two species (bloater and alewife) had two size classes. At each site and season 20 fish were collected in the following categories: small bloater (< 160 mm), large bloater (> 160 mm), small alewife (60-120 mm), large alewife (> 120 mm), rainbow smelt (>100 mm), slimy sculpins, and deepwater sculpins. Because the age of bloater chubs was not known in the field, a length cut-off based on sampling in recent years was used to obtain an approximate separation by age into the specified age categories for chubs of 0-2 years and 4+ years of age. At least ten fish were analyzed in each sample. However, if more than three fish had empty stomachs, the other ten fish were analyzed. In a few cases (as with sculpins), all fish collected were analyzed to provide information on a poorly studied species.

Collecting Forage Fish and Zooplankton

Fish were captured with a midwater or bottom trawl. Captured fish were identified to species and counted. Each sample was placed in labelled plastic bags and then deep-frozen. Frozen fish were transported to BRD-Great Lakes Science Center on ice in coolers to the laboratory freezer.

To provide availability of food for forage fish, zooplankton samples were taken concurrently with fish samples at the three sites and seasons. A stratified sampling regime for zooplankton was used to typify zooplankton availability. A Puget Sound style closing net with 160 u mesh and 50 cm diameter mouth was used in taking stratified vertical zooplankton tows. Samples were stratified by depth in two to three ecological strata -- epilimnion, metalimnion, and hypolimnion -- depending on time of year and breadth of metalimnion. Two replicates were taken per sample. Comparisons of zooplankton abundance with fish diet will detail whether fish are consuming prey based on availability or are showing preferences for certain species or size ranges of prey.

Zooplankton samples in the cod end of the net were placed into collection along with an alka-seltzer tablet (narcotizing and buffering agent). Each sample was washed from the bucket with distilled water into a 1 quart sample jar. Buffered and sugared formalin (2 g Borax/100 ml and 4 g sucrose/100 ml with 8 mg Phloxine B dye/l formalin added to enhance visibility of zooplankton) was added such that each sample contains 5% formalin by volume. Zooplankton samples were transported to the Great Lakes Science Center. Integrity of samples were checked upon arrival to laboratory.

Analyzing Forage Fish Diets and Zooplankton Abundance

Stomach contents of forage fish and zooplankton availability were analyzed in the laboratory at Great Lakes Science Center. Fish were thawed under cool water and individually weighed to the nearest gram and measured to the nearest millimeter and provided individual numbers. Stomachs were removed using surgical scissors (from esophagus to pyloric caecum). The stomach was then preserved in 10% formalin. We also determined the sex of the individual fish if possible. At a later date the stomachs were opened and contents removed completely. Contents were teased apart and assessed as to whether they could be completely counted or needed to be subsampled. All large prey (such as *Mysis*, *Bythotrephes*, and amphipods) were counted completely. Contents to be subsampled were diluted to a known volume (usually 100 ml), gently stirred, and a ten percent subsample was removed. The contents were then identified to the lowest possible taxon, enumerated, and measured with aid of a Ward counting wheel under a dissecting microscope with an ocular micrometer. Up to ten individuals per taxon per fish were measured to the nearest micron. Length measurements were converted to biomass estimates with regressions (Appendix A).

Each zooplankton sample was strained and drained of formalin. If subsampling was necessary, the sample was diluted with water of a known volume, stirred to provide a consistent density of plankton, and then subsampled (4-ml). The subsample was returned to the original sample after processing and the procedure was repeated for a total of three subsamples. Certain taxa (such as *Mysis*, *Bythotrephes*, and amphipods) were considered too large to be subsampled; all were removed by hand using the naked eye or a magnifying light, and then processed in the same manner. The zooplankters were identified to lowest possible taxon, enumerated, and measured with aid of a Ward counting wheel under a dissecting microscope with an ocular micrometer. Most mature specimens could be identified to genus and species; most immatures could be identified to family or genus. Specimens smaller than rotifers (<100 microns) were not counted. Up to ten individuals per species per station were measured to the nearest micron. Length measurements were converted to biomass estimates with regressions (Appendix A). The three subsample counts were averaged and the resulting mean was used to calculate number of organisms per cubic meter.

RESULTS AND DISCUSSION

An important step in understanding the community and contaminant dynamics of Lake Michigan is to examine the lower trophic level interactions of forage fishes and their main prey, invertebrates. Competition for food and habitat may be important in determining the forage fish community, and even though the diet relationships of nearshore forage fish communities have been studied (Crowder et al. 1981), the same has not been done for the open water. Of the five major open water forage fish species large bloater were consistently the largest group caught throughout this study, both in terms of length and weight, and large alewives were the next largest (Tables 1 and 2). Small bloater and rainbow smelt were similar in length, however, small bloater were almost always heavier, sometimes more than twice the weight. Deepwater sculpins were most similar in size to small bloaters and rainbow smelt. Small alewives and slimy sculpins were consistently the smallest fish, with slimy sculpins generally heavier per length.

The fullness index provides some measure of the feeding intensity. Small alewives had the highest mean percent fullness index (average of 1.99), followed by large alewives, and both sculpin species (≈ 1.2). Bloaters had the lowest mean percent fullness index (≈ 0.7) in comparison to the other fish. In this study no real pattern was shown seasonally or by site. These values may be useful to develop power functions to test for size-related changes in predator success as a measure of food limitation (Kraft and Kitchell 1986).

The diet of large alewives mainly consisted of three major taxonomic groups, zooplankton, *Diporeia*, and *Mysis* (Figure 1); however, *Bythotrephes* supplanted *Diporeia* as a dominant food item in fall of 1995. No consistent trends in proportions were found between sites or seasons. Zooplankton were important throughout the study, *Diporeia* were important in the summer and spring, and *Mysis* were important in the spring and fall, particularly at Port Washington. Janssen and Brandt (1980) reported *Mysis* as the most important prey item for alewives. However, this finding was prior to the recovery of bloater populations throughout Lake Michigan in the 1980's (Eck and Wells 1987) and abundant bloater populations since may have affected alewife distribution patterns (Crowder and Magnuson 1982). Alewives ate well throughout the study as only 4 of 145 fish sampled were empty (Tables 1 and 2). Alewives also had the most diverse diet of any of the fishes, many having over twenty different taxa in their stomachs. Since they are capable of filtering as well as particulate feeding (Crowder and Binkowski 1983) alewives are able to feed more efficiently on a wider array of prey. Of all the planktivores, alewives seem to make the most use of *Bythotrephes* (Keilty 1990). The four collections where percent biomass intake was low (at Port Washington in spring 1994, and Saugatuck in fall of 1994 and in spring 1995, and Sturgeon Bay in fall 1995) were due to large numbers of *Bythotrephes* caudal spines in the foregut. These spines were quantified as non-food items as we believe they had accumulated from previous meals. Since *Bythotrephes* are not alive in the spring, those spines present at that time could only have either been retained from the fall or possibly ingested from off the substrate while foraging. In the fall, we found many more spines in the gut than other body parts of *Bythotrephes*. As with other cladocerans, this disparity may indicate an instance of differential digestion rates (Gannon 1976).

Small alewives mainly ate zooplankton and *Diporeia* (Figure 2); unlike large alewives they ate few *Mysis* or *Bythotrephes*. As small alewives were caught nearshore, they may not forage offshore enough to encounter *Mysis* or *Bythotrephes.* Alternatively, they may be too small to consistently ingest either species. Small alewives ate as well as the larger ones, with only 4 empty fish out of 135 sampled (Tables 1 and 2), and also had a very diverse diet. The proportion of prey items in their guts were fairly similar between years, except for some differences at Sturgeon Bay. One large anomaly in the diet of the summer fish occurred at Saugatuck, where one specimen in the sample ate about nine hundred fish eggs (probably of some small cyprinid), but, it was not the only instance of small alewives eating fish eggs. Alewives are seen as potential predators on the pelagic eggs of emerald shiner, and have been implicated in their decline in the 1960's (Stewart et al. 1981). Small alewives were the most difficult group to sample as shown by the absence of captures at Saugatuck in spring and at Port Washington in the summer 1994; the shallowness of their preferred habitat probably contributing to this sampling problem. Although small alewives may seem to be habitat limited, their importance to the flow of resources should not be discounted; YOY and yearling alewives were found to account for well over 50% of total zooplankton consumption by alewives in Lake Michigan (Hewett and Stewart 1989).

In contrast to small alewives, large bloaters were the easiest group of fish to catch, as they were in almost all trawls and caught in association with most other groups; as of now, they are the dominant forage fish species in Lake Michigan (Eck and Wells 1987, McDonald et al. 1990). Their diets were dominated by *Diporeia* and *Mysis* with only a few instances of other items (zooplankton, *Bythotrephes*, fish eggs) in their diet (Figure 3). Historically *Diporeia* and *Mysis* have been their staple foods (Wells and Beeton 1963, Crowder and Crawford 1984). In fact, the great increase in bloater numbers seems to be responsible for a corresponding decrease in the abundance of *Mysis* and *Diporeia* (McDonald et al. 1990). The diets at Port Washington were dominated by *Mysis* whereas *Diporeia* was more important at Saugatuck and Sturgeon Bay. The small increase in non-food items at Sturgeon Bay in fall 1994 is attributable to *Bythotrephes* spines either left over from previous meals or ingested off the bottom (Keilty 1990). Large bloater did not seem to eat as well as alewives, with 46 empty of the 212 fish sampled. Most of the empty fish (33) were in spring (Tables 1 and 2). High incidence of empty stomachs may also indicate that their peak feeding times are different from alewives.

Small bloaters were similar to large bloaters in that there were many empty stomachs--55 empty of 171 sampled and 42 of those in spring (Tables 1 and 2). Also similar to small alewives, small bloaters were difficult to collect. We could find none to sample at Sturgeon Bay in spring and Port Washington in fall 1995 (Figure 4), and a few times we had to increase the upper size limit in order to catch a sufficient amount. Small bloater ate mostly *Diporeia*, but also large amounts of *Mysis* and zooplankton. At Sturgeon Bay in fall 1994 their diet was completely *Bythotrephes*. The only consistency in their diet was that spring and summer diets of 1994 were fairly similar. Small bloaters showed similarities in diet at times with large alewife and rainbow smelt. Crowder and Magnuson (1982) describe small bloater diets as being similar to diets of alewife and rainbow smelt.

Rainbow smelt diets were relatively simple and straightforward. *Mysis* greatly predominated in the diet, especially in the spring (Figure 5). However, zooplankton, *Diporeia*, and young fish were also eaten throughout the study. The number of fish eaten was not great but they contributed substantially to the biomass eaten. Fish eaten were mainly young alewives, although some may have been young bloater. Alewives have been implicated as a possible predator on young fish (Eck and Wells 1987) and could probably have quite a particular impact on the larval stage. However, this study seems to point to rainbow smelt as an even greater threat, with more of an impact on a greater size range of young fish; their sharp canine teeth were designed for grasping such prey (Kendall 1926, Lagler et al. 1977). YOY rainbow smelt feed far sooner on *Mysis* and *Diporeia* than YOY alewives of a similar size (Urban and Brandt 1993), however, this coincides with a habitat shift to deeper water as well. Rainbow smelt were similar to bloater in how well they fed with 52 empty out of 201 sampled; half of the empty were in spring of 1995 (Tables 1 and 2). Timing of our spring sampling may have coincided with the smelt spawning season.

Sculpin diets were very similar to those previously described in Lake Michigan (Kraft and Kitchell 1986), and in Lake Superior (Selgeby 1988). The great bulk of the diets of deepwater sculpin and slimy sculpin consisted of *Diporeia* (Figures 6 and 7). Both species also ate fish eggs, apparently sculpin eggs, throughout the year. The major difference between the two sculpin species is that deepwater sculpin made much greater and consistent use of *Mysis* than did slimy sculpins. This observation was not surprising as deepwater sculpin were larger (about 1. 2/3 times) than slimy sculpins (Tables 1 and 2) and should be better able to capture the larger prey. Kraft and Kitchell (1986) attributed the failure of slimy sculpins to feed upon *Mysis* as a combination of prey behavior, predator sensory abilities and predator behavior; however, the failure of slimy sculpins to feed on large *Diporeia* was attributed to handling constraints with larger prey. We processed all the deepwater sculpins we caught (455) as diet data on them is limited in the literature, and only 9 were empty. We processed 400 slimy sculpins and found only 21 empty fish. Both species had *Bythotrephes* caudal spines in their stomachs and were probably picked off the substrate. They also contained various amounts of gravel and algal detritus.

Diet overlap among the groups of forage fish was usually very low (Table 3), but, overlap values between large and small alewives and large and small bloaters were very high. We combined the size categories for both alewives and bloaters in calculating overlap values. Another study done on Lake Michigan in 1993 (unpublished data - GLSC) showed high diet overlap among alewives, bloaters, and smelt in the spring, in particular between size categories, but, these values declined thru summer and fall. Alewives had the lowest overlap with all other species with rainbow smelt having the highest overlap them at only 27%. This finding is in contrast to Crowder et al. (1981) who found extremely high diet overlap between alewives and rainbow smelt during the day. They felt that the similarities in diet were tempered by differences in habitat, thereby mitigating any possible competition. This habitat partitioning was probably the same strategy for adult and young alewives and bloater, along with differences in size of prey. Young of both alewife and bloater inhabit shallower water than do the adults (Wells 1968, Crowder et al. 1981, Crowder and Magnuson 1982, Crowder and Binkowski 1983). Deepwater and slimy sculpins had the only really significant diet overlap at 78%, which might be expected as both species dwell on the bottom and have a limited availability of food types. Although there is some overlap their distributions are largely disjunct as deepwater sculpin reside at greater depths (Wells 1968, Kraft and Kitchell 1986).

In summary, there appears to be a partitioning of the resources among the forage fish in Lake Michigan. Even when there was a high similarity in diet between groups the habitat differences would limit potential competition. Such partitioning of resources is common among fish assemblages (Crowder et al. 1981, Ross 1986, Urban and Brandt 1993). All groups of fish were similar in that *Diporeia hoyi* and to a lesser extent, *Mysis relicta*, were important in their diet by weight at sometime during the study. Bloater mainly consumed *D. hoyi* and *M. relicta*, although zooplankton were also eaten. Alewives mainly consumed zooplankton, but in addition made extensive use of *D. hoyi*. Rainbow smelt heavily consumed *M. relicta*, but also made use of zooplankton and young fish. *D. hoyi* was the dominant food item in the diet of both sculpin species, but deepwater sculpin ate *M. relicta* to a far greater extent than did slimy sculpin. Both sculpin species also made use of fish eggs. Slimy sculpins had the least diverse diet in terms of number of taxa eaten whereas alewives had the most diverse diet. Only the diets of sculpins were consistent between sites and years. Most fish diets were more diverse in the summer and fall, reflecting use of a broader range of thermal habitats and more diverse zooplankton population.

REFERENCES

Crowder, L. B., and F. P. Binkowski. 1983. Foraging behaviors and the interaction of alewife, *Alosa pseudoharengus*, and bloater, *Coregonus hoyi*. Env. Biol. Fish. 8: 105-113.

Crowder, L. B., and H. B. Crawford. 1984. Ecological shifts in resource use by bloaters in Lake

Michigan. Trans. Am. Fish. Soc. 113: 694-700.

Crowder, L. B., and J. J. Magnuson. 1982. Thermal habitat shifts by fishes at the thermocline in Lake Michigan. Can. J. Fish. Aquat. Sci. 39: 1046-1050.

Eck, G. W., and L. Wells. 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of the alewife (*Alosa pseudoharengus*). Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 53-60.

Gannon, J. E. 1976. The effects of differential digestion rates of zooplankton by alewife, *Alosa pseudoharengus*, on determinations of selective feeding. Trans. Am. Fish. Soc. 105:89-95.

Hewett, S. W., and D. J. Stewart. 1989. Zooplanktivory by alewives in Lake Michigan: ontogenetic, seasonal, and historical patterns. Trans. Amer. Fish. Soc. 118: 581-596.

Janssen, J., and S. B. Brandt. 1980. Feeding ecology and vertical migration of adult alewives *Alosa pseudoharengus* in Lake Michigan. Can. J. Fish. Aquat. Sci. 37: 177-184.

Keilty, T. J. 1990. Evidence for alewife (*Alosa pseudoharengus*) predation on the European cladoceran *Bythotrephes cederstroemi* in northern Lake Michigan. J. Great Lakes Res. 16(2): 330-333.

Kendall, W. C. 1926. The smelts. Bull. U.S. Bur. Fish. 42: 217-375.

Kraft, C. E., and Kitchell, J. F. 1986. Partitioning of food resources by sculpins in Lake Michigan. Env. Biol. Fishes 16(4): 309-316.

Lagler, K. F., J. E. Bardach, R. R. Miller, and D. R. M. Passino. 1977. Ichthyology. 2nd Ed. John Wiley & Sons. New York. 505pp.

McDonald, M. E., L. B. Crowder, and S. B. Brandt. 1990. Changes in *Mysis* and *Pontoporeia* populations in southeastern Lake Michigan: A response to shifts in the fish community. Limnol. Oceanogr. 35: 220-227.

Ross, S. T. 1986. Resource partitioning in fish assemblages: A review of field studies. Copeia. 1986: 352-388.

Selgeby, J. H. 1988. Comparative biology of the sculpins of Lake Superior. J. Great Lakes Res. 14:44-51.

Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans. Amer. Fish. Soc. 110: 751-763.

Urban, T. P., and S. B. Brandt. 1993. Food and habitat partitioning between young-of-year alewives and rainbow smelt in southeastern Lake Ontario. Env. Biol. Fish. 36:359-372.

Wells, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. Fish. Bull. 67(1): 1-15.

Wells, L., and A. M. Beeton. 1963. Food of the bloater, *Coregonus hoyi*, in Lake Michigan. Trans. Am. Fish. Soc. 92: 245-255.

Table 1. Mean length (mm)(±SE), mean weight (g)(±SE), mean fullness index (%)(±SE), and number of fish with food and number empty at each Lake Michigan site (port) in 1994. The means include all fish analyzed from that sampling period (i.e., with or without food).

Species	Mean Length	Mean Weight	Mean Fullness Index	Number with food-Number empty
			Spring	
			Saugatuck	
Large Bloater	199.1(±4.91)	61.2(±5.14)	1.15008(±0.22771)	22 - 8
Small Bloater	140.9(±4.51)	20.4(±1.50)	0.36856(±0.10154)	12 - 8
Large Alewife	175.9(±5.60)	40.7(±3.62)	2.18836(±0.34568)	10 - 0
Small Alewife				0 - 0
Rainbow Smelt	121.1(±4.52)	9.6(±1.16)	0.58339(±0.12850)	7 - 3
Deepwater Sculpin	105.7(±8.71)	15.3(±2.79)	1.43837(±0.35567)	18 - 1
Slimy Sculpin	72.2(±1.80)	4.3(±0.30)	1.21825(±0.24043)	10 - 0
			Port Washington	
Large Bloater	208.6(±7.39)	68.1(±7.30)	0.84954(±0.18685)	8 - 2
Small Bloater	149.3(±1.58)	21.8(±0.67)	1.31683(±0.20123)	10 - 10
Large Alewife	146.8(±3.26)	23.7(±1.75)	1.38726(±0.38860)	9 - 1
Small Alewife	77.0(±2.85)	3.1(±0.33)	1.89207(±0.24549)	9 - 1
Rainbow Smelt	125.8(±4.66)	10.9(±1.60)	0.88800(±0.17119)	8 - 2

Deepwater Sculpin	123.8(±3.52)	21.9(±2.02)	1.18714(±0.15636)	20 - 0
Slimy Sculpin	72.0(±4.36)	5.2(±1.18)	0.75819(±0.16139)	10 - 1
		Sturgeon Bay		
Large Bloater	201.2(±4.84)	71.0(±6.02)	0.88597(±0.17843)	18 - 1
Small Bloater	160.8(±1.46)	30.4(±1.19)	1.72656(±0.29442)	8 - 2
Large Alewife	177.2(±8.93)	37.9(±5.16)	2.83253(±0.66785)	10 - 0
Small Alewife	82.8(±3.56)	4.1(±0.69)	1.70627(±0.21193)	20 - 0
Rainbow Smelt	125.7(±3.96)	10.6(±0.92)	0.81385(±0.15616)	13 - 7
Deepwater Sculpin	92.3(±9.08)	12.8(±3.07)	1.95950(±0.38833)	19 - 1
Slimy Sculpin	54.3(±4.38)	2.8(±0.67)	1.04900(±0.17980)	16 - 0
		Summer		
		Saugatuck		
Large Bloater	186.8(±2.95)	48.3(±2.55)	0.46572(±0.08649)	10 - 0
Small Bloater	154.5(±4.89)	26.8(±2.26)	0.94314(±0.10453)	10 - 0
Large Alewife	191.5(±6.54)	43.6(±3.92)	0.49681(±0.10660)	10 - 0
Small Alewife	106.9(±2.35)	9.3(±0.73)	1.55859(±0.12524)	10 - 0
Rainbow Smelt	147.1(±4.98)	16.5(±1.81)	1.04420(±0.11723)	10 - 0
Deepwater Sculpin	100.1(±5.80)	14.9(±1.89)	1.51117(±0.11888)	29 - 1

Slimy Sculpin	70.8(±2.82)	5.0(±0.71)	1.62677(±0.24271)	10 - 0
		Port Washington		
Large Bloater	183.9(±5.54)	46.0(±5.69)	0.45911(±0.08634)	8 - 2
Small Bloater	147.0(±2.81)	24.2(±1.21)	0.25872(±0.04595)	7 - 3
Large Alewife	180.4(±6.64)	40.2(±3.20)	1.01371(±0.26073)	10 - 0
Small Alewife				0 - 0
Rainbow Smelt	132.8(±2.89)	13.3(±0.72)	0.80294(±0.13038)	14 - 6
Deepwater Sculpin	125.6(±4.10)	22.9(±2.34)	1.45822(±0.24538)	20 - 0
Slimy Sculpin	72.3(±4.68)	5.8(±0.93)	1.63045(±0.22728)	10 - 0
		Sturgeon Bay		
Large Bloater	184.4(±4.58)	51.0(±4.12)	1.27189(±0.28552)	10 - 0
Small Bloater	120.5(±6.83)	14.3(±2.63)	2.11504(±0.50717)	10 - 0
Large Alewife	184.4(±3.89)	37.8(±2.23)	1.09616(±0.20497)	10 - 0
Small Alewife	76.8(±1.70)	2.4(±0.18)	2.09273(±0.35135)	9 - 0
Rainbow Smelt	124.5(±6.01)	10.7(±1.57)	0.55485(±0.09881)	7 - 3
Deepwater Sculpin	99.1(±4.85)	14.0(±1.73)	0.78380(±0.10039)	27 - 2
Slimy Sculpin	57.9(±3.98)	3.0(±0.66)	0.51943(±0.13191)	8 - 6

		Fall		
		Saugatuck		
Large Bloater	195.0(±5.73)	70.9(±6.90)	0.24366(±0.08207)	8 - 2
Small Bloater	148.1(±2.61)	27.3(±1.92)	0.35063(±0.11795)	7 - 3
Large Alewife	171.0(±2.37)	40.1(±1.77)	1.69828(±0.15099)	9 - 1
Small Alewife	77.2(±1.56)	3.3(±0.20)	1.56956(±0.58850)	10 - 0
Rainbow Smelt	127.9(±1.43)	12.2(±0.45)	0.23968(±0.03729)	9 - 1
Deepwater Sculpin	115.4(±3.71)	20.4(±1.76)	0.90726(±0.10819)	33 - 1
Slimy Sculpin	68.9(±3.30)	5.5(±0.59)	1.72215(±0.19090)	30 - 1
		Port Washington		
Large Bloater	198.8(±4.73)	76.8(±6.21)	0.71404(±0.17268)	15 - 4
Small Bloater	148.6(±2.21)	25.7(±0.99)	0.70518(±0.31106)	9 - 1
Large Alewife	177.6(±5.12)	53.1(±5.14)	1.24697(±0.14223)	9 - 0
Small Alewife	86.8(±3.01)	6.3(±0.73)	3.77538(±0.40883)	10 - 0
Rainbow Smelt	130.2(±3.42)	13.4(±1.18)	2.36730(±0.30994)	10 - 0
Deepwater Sculpin	126.9(±4.77)	26.5(±2.92)	0.87919(±0.18882)	19 - 0
Slimy Sculpin	65.5(±1.44)	4.1(±0.31)	1.34086(±0.11122)	68 - 1
		Sturgeon Bay		

Large Bloater	189.5(±8.25)	68.1(±8.98)	0.81142(±0.15170)	13 - 1
Small Bloater	147.4(±1.52)	23.7(±0.78)	0.22404(±0.07886)	8 - 2
Large Alewife	163.0(±4.56)	30.9(±4.72)	2.33820(±0.38967)	10 - 0
Small Alewife	88.6(±1.73)	5.4(±0.29)	2.66171(±0.30835)	10 - 0
Rainbow Smelt	140.7(±4.07)	18.2(±1.70)	1.26348(±0.43146)	8 - 2
Deepwater Sculpin	124.1(±3.45)	25.0(±1.73)	0.83324(±0.10915)	25 - 0
Slimy Sculpin	76.9(±4.05)	7.3(±1.24)	1.38073(±0.21020)	11 - 0

Table 2. Mean length (mm)(±SE), mean weight (g)(±SE), mean fullness index (%)(±SE), and number of fish with food and number empty at each Lake Michigan site (port) in 1995. The means include all fish analyzed from that sampling period (i.e., with or without food).

Species	Mean Length	Mean Weight	Mean Fullness Index	Number with food-Number empty
		Spring		
		Saugatuck		
Large Bloater	253.2(±9.37)	139.4(±21.06)	0.72235(±0.21791)	8 - 2
Small Bloater	156.7(±1.59)	24.8(±0.79)	0.51204(±0.20589)	11 - 9
Large Alewife	179.4(±6.54)	44.8(±4.70)	0.93028(±0.20455)	10 - 1
Small Alewife	103.9(±2.26)	8.3(±0.68)	0.62031(±0.13118)	9 - 1
Rainbow Smelt	131.9(±3.77)	15.1(±1.47)	0.57425(±0.17520)	8 - 12
Deepwater Sculpin	133.4(±2.50)	25.8(±1.56)	0.98469(±0.08859)	30 - 0
Slimy Sculpin	68.4(±3.21)	4.5(±0.63)	1.45810(±0.13021)	28 - 2
		Port Washington		
Large Bloater	205.1(±3.93)	72.3(±5.04)	0.27706(±0.07197)	10 - 10
Small Bloater	156.3(±1.53)	27.6(±0.81)	0.19275(±0.07557)	8 - 13
Large Alewife	168.9(±5.54)	38.8(±3.45)	0.33299(±0.06391)	8 - 1
Small Alewife	95.4(±2.16)	6.6(±0.73)	1.12057(±0.23330)	8 - 2
Rainbow Smelt	121.8(±9.12)	13.1(±2.33)	1.51988(±0.29413)	15 - 1
Deepwater Sculpin	117.7(±3.32)	19.4(±1.65)	0.84431(±0.08527)	39 - 1

Slimy Sculpin	65.4(±1.64)	3.8(±0.29)	1.17534(±0.17496)	45 - 4
		Sturgeon Bay		
Large Bloater	217.5(±3.00)	92.8(±5.57)	0.63164(±0.18083)	10 - 10
Small Bloater				0 - 0
Large Alewife	186.8(±5.38)	52.6(±5.16)	0.67543(±0.12147)	10 - 0
Small Alewife	82.7(±1.58)	3.5(±0.21)	1.10238(±0.18181)	10 - 0
Rainbow Smelt	143.2(±3.41)	17.4(±1.41)	0.28629(±0.11062)	8 - 12
Deepwater Sculpin	112.9(±4.88)	20.8(±2.20)	1.01682(±0.12223)	39 - 1
Slimy Sculpin	53.4(±2.26)	2.6(±0.38)	1.52635(±0.14772)	37 - 3
		Fall		
		Saugatuck		
Large Bloater	192.9(±6.79)	56.9(±7.20)	0.37991(±0.08679)	10 - 0
Small Bloater	161.7(±1.64)	30.7(±1.30)	0.22309(±0.06371)	7 - 3
Large Alewife	168.7(±5.65)	50.0(±2.21)	0.90089(±0.14471)	10 - 0
Small Alewife	74.1(±2.00)	3.6(±0.33)	3.16596(±0.49596)	10 - 0
Rainbow Smelt	117.3(±6.17)	9.8(±1.47)	0.69210(±0.17562)	10 - 0
Deepwater Sculpin	111.8(±3.89)	19.7(±1.61)	1.10039(±0.09254)	49 - 1
Slimy Sculpin	83.6(±1.89)	7.8(±0.57)	1.33978(±0.10302)	32 - 0

		Port Washington		
Large Bloater	206.2(±5.15)	77.2(±7.67)	0.91280(±0.25814)	8 - 2
Small Bloater				0 - 0
Large Alewife	180.9(±4.75)	48.7(±3.93)	0.77664(±0.14766)	10 - 0
Small Alewife	72.4(±2.73)	2.8(±0.33)	3.07073(±0.59606)	10 - 0
Rainbow Smelt	150.8(±3.41)	20.7(±1.83)	2.72200(±0.75946)	8 - 2
Deepwater Sculpin	116.5(±3.31)	22.4(±1.92)	1.22545(±0.10414)	51 - 0
Slimy Sculpin	66.0(±2.35)	4.3(±0.49)	1.30865(±0.10809)	35 - 2
		Sturgeon Bay		
Large Bloater	214.7(±4.04)	89.7(±7.55)	0.48917(±0.27386)	8 - 2
Small Bloater	88.0(±2.99)	4.7(±0.52)	0.42605(±0.10175)	9 - 1
Large Alewife	152.5(±5.29)	29.3(±3.03)	0.81307(±0.15973)	10 - 0
Small Alewife	90.9(±1.46)	6.0(±0.37)	1.59162(±0.24095)	10 - 0
Rainbow Smelt	133.5(±3.31)	14.2(±1.26)	1.50820(±0.35396)	14 - 1
Deepwater Sculpin	97.5(±4.99)	13.2(±2.18)	1.87681(±0.19210)	28 - 0
Slimy Sculpin	50.3(±1.88)	1.8(±0.21)	1.25353(±0.11970)	29 - 1

Table 3. Mean percent diet overlap of forage fish during Lake Michigan Mass Balance study 1994-5. The two size categories for both bloater and alewife were combined to calculate these values.

	Bloater	Alewife	R. Smelt	D. Sculpin	S. Sculpin
Bloater	-	17.6	37.4	42.8	41.7
Alewife	17.6	-	27.7	4.3	5.0
Rainbow Smelt	37.4	27.7	-	12.6	6.8
Deepwater Sculpin	42.8	4.3	12.6	-	78.2
Slimy Sculpin	41.7	5.0	6.8	78.2	-

Figure 1. Diet by percent biomass of large alewives in Lake Michigan at sites near Saugatuck, MI., Port Washington, WI., and Sturgeon Bay, WI. in 1994 and 1995.

Figure 2. Diet by percent biomass of small alewives in Lake Michigan at sites near Saugatuck, MI., Port Washington, WI., and Sturgeon Bay, WI. in 1994 and 1995.

Figure 3. Diet by percent biomass of large bloater in Lake Michigan at sites near Saugatuck, MI., Port Washington, WI., and Sturgeon Bay, WI. in 1994 and 1995.

Figure 4. Diet by percent biomass of small bloater in Lake Michigan at sites near Saugatuck, MI., Port Washington, WI., and Sturgeon Bay, WI. in 1994 and 1995.

Figure 5. Diet by percent biomass of rainbow smelt in Lake Michigan at sites near Saugatuck, MI., Port Washington, WI., and Sturgeon Bay, WI. in 1994 and 1995.

Figure 6. Diet by percent biomass of deepwater sculpins in Lake Michigan at sites near Saugatuck, MI., Port Washington, WI., and Sturgeon Bay, WI. in 1994 and 1995.

Figure 7. Diet by percent biomass of slimy sculpins in Lake Michigan at sites near Saugatuck, MI., Port Washington, WI., and Sturgeon Bay, WI. in 1994 and 1995.

Figure 8. Density (number/m^3) of zooplankton in Lake Michigan at sites near Saugatuck, MI., Port Washington, WI., and Sturgeon Bay, WI. in 1994 and 1995. Numbers underneath each group of bars indicate the bottom depth sampled above.

Appendix A

Length - dry weight regressions and conversion factors used for prey in diets of forage fish in Lake Michigan in 1994-95.

PREY TAXON (ID#)	CONVERSION FACTOR	SOURCE
Rotifera	$W(\mu g) = 0.2$	Nalepa and Quigley (1980)
Asplanchna	$W(\mu g) = .28\text{--}1.5$ (range)	Dumont et al. (1975)
Nematoda	$W(\mu g) = 0.1$	Nalepa and Quigley (1980)
Bryozoa	$W(\mu g) = 0.3$	***
Tardigrada	$W(\mu g) = 0.3$	Nalepa and Quigley (1980)
Oligochaeta	$W(\mu g) = 60$ per cm	Nalepa and Quigley (1980)
Eurycercus lamellatus	$W(\mu g) = 11.1$	Nalepa and Quigley (1980)
Chydorus sphaericus	$W(\mu g) = 14.0793L(mm)^{1.9796}$	Culver et al. (1985)
Alona	$W(g) = 3.264L(mm) - 4.468$	Rosen (1981) **
Acroperus harpae	$W(\mu g) = 0.00905L(\mu m)^{0.85}$	Dumont et al. (1975)
Pleuroxus	$W(\mu g) = 35.6L(mm)^{4.03}$	Dumont et al. (1975)
Alonella	$W(\mu g) = 1.35\text{x}10^{-6}L\ (\mu m)^{2.26}$	Dumont et al. (1975)
Diaphanosoma	$W(\mu g) = 5.0713L(mm)^{1.0456}$	Culver et al. (1985)
Sida crystallina	$W(g) = 2.189L(mm) - 5.108$	Rosen (1981) **
Moina	$\ln W(\mu g) = 1.75 + 2.65 \ln L(mm)$	Hart (1987)
Scapholeberis	$W(g) = 3.079L(mm) - 4.753$	Rosen (1981) **
Simocephalus	$W(\mu g) = 4.0L(mm)^{3.81}$	Dumont et al. (1975)
Ceriodaphnia	$W(\mu g) = 4.0216L(mm)^{1.9763}$	Culver et al. (1985)
Daphnia pulex (pulicaria)	$\log W(\mu g) = 0.744L(mm) + 0.076$ $W(\mu g) = 2.4\text{x}10^{-8}L\ (\mu m)^{2.77}$	Edmondson (1955) Dumont et al. (1975)
Daphnia galeata	$W(\mu g) = 7.4997L(mm)^{1.5644}$	Culver et al. (1985)
Daphnia retrocurva	$W(\mu g) = 3.7847L(mm)^{2.6807}$	Culver et al. (1985)
Daphnia longiremis	$W(\mu g) = 3.7847L(mm)^{2.6807}$	***
Bosmina	$W(\mu g) = 17.7369L(mm)^{2.2291}$	Culver et al. (1985)

Eubosmina	$W(\mu g) = 21.9128L(mm)^{2.3371}$	Culver et al. (1985)
Ophryoxus gracilis	$W(\mu g) = 7.4997L(mm)^{1.5644}$	***
Holopedium	$W(\mu g) = 6.4$	Hawkins and Evans (1979)
Leptodora kindtii	$W(\mu g) = 1.5605L(mm)^{1.8730}$	Culver et al. (1985)
Polyphemus pediculus	$W(g) = 2.152L(mm) - 4.793$	Rosen (1981)**
Bythotrephes cederstroemi	$\log W(\mu g) = 1.617 + 1.514 \log SL(mm)$ $\log W(\mu g) = 1.428 + 1.67 \log SL(mm)$ $\log W(\mu g) = -.053 + 2.12 \log TL(mm)$	Garton et al. (1990) λ Garton and Berg (1990) Makarewicz and Jones (1990)
Copepod nauplii (all)	$W(\mu g) = 3.0093L(mm)^{1.7064}$	Culver et al. (1985)
Calanoid copepodite	$W(\mu g) = 4.5921L(mm)^{1.7034}$	Culver et al. (1985) *
Epischura	$W(\mu g) = 9.9$	Hawkins and Evans (1979)
Skistodiaptomus	$W(\mu g) = 6.1927L(mm)^{1.9604}$	Culver et al. (1985) *
Leptodiaptomus ashlandi	$W(\mu g) = 7.3614L(mm)^{3.8564}$	***
Leptodiaptomus minutus	$W(\mu g) = 7.3614L(mm)^{3.8564}$	Culver et al. (1985) *
Leptodiaptomus sicilis	$W(\mu g) = 14.9$	Hawkins and Evans (1979)
Eurytemora	$W(\mu g) = 9.9$	Nalepa and Quigley (1980)
Limnocalanus	$\log W(\mu g) = 0.98L(mm) - 0.79$	Conway (1977)
Senecella	$\log W(\mu g) = 0.98L(mm) - 0.79$	***
Cyclopoid copepodite	$W(\mu g) = 5.6713L(mm)^{1.9347}$	Culver et al. (1985) *
Diacyclops thomasi	$W(\mu g) = 5.6713L(mm)^{1.9347}$	Culver et al. (1985) *
Acanthocyclops vernalis	$W(\mu g) = 7.0729L(mm)^{2.5563}$	Culver et al. (1985) *
Mesocyclops	$W(\mu g) = 6.6586L(mm)^{2.8945}$	Culver et al. (1985) *
Macrocyclops	$W(\mu g) = 6.6586L(mm)^{2.8945}$	***
Eucyclops	$W(\mu g) = 4.6$	Nalepa and Quigley (1980)
Tropocyclops / M. varicans / D. nanus	$W(\mu g) = 0.9$	Nalepa and Quigley (1980)

Harpacticoida	W(μg) = 3.2	Nalepa and Quigley (1980)
Ostracoda	W(μg) = 21.2	Nalepa and Quigley (1980)
Diporeia	$W(mg) = 0.0067L^{3.0232}$	Winnell and White (1984)
Mysis	log W(mg) = -2.68 + 2.86 log L	Shea and Makarewicz (1989)
Terrestrial Insect	$W(mg) = 0.0305L(mm)^{2.62}$	Rogers et al. (1976)
Chironomidae (*P. scaleum*)	log W(μg) = 1.089 + 2.319 log L	Nalepa and Quigley (1980)
Chironomidae (*Heterotrissocladius*)	log W(μg) = 0.8129 + 2.1946 log L	Nalepa and Quigley (1980)
Chironomidae pupae	W(mg) = .2296	Meyer (1989)
Ceratopogonidae (*Palpomyia*)	ln W(mg) = -5.714 + 2.39 ln L(mm)	Smock (1980)
Chaoborus	ln W(mg) = -7.70 + 2.43 ln L(mm)	Eaton (1983)
Ephemeroptera (*Caenis*)	ln W(mg) = -4.976 + 2.61 ln L(mm)	Smock (1980)
Corixidae (*Sigara*)	ln W(mg) = -3.27 + 2.53 ln L(mm)	Smock (1980)
Odonata (*Argia*)	ln W(mg) = -4.756 + 2.67 ln L(mm)	Smock (1980)
Acarina	W(mg) = .1047	Meyer (1989)
Zebra mussel larva	$W(ng) = 58.207 - 2.636L + 0.037L^2(\mu m)$ @	Sprung (1993) from Hillbricht-Ilkowska and Stanczykowska('69)
Clam (Pisididae)	W(μg) = 94.2	Nalepa and Quigley (1980)
Turbellaria	W(μg) = 3.5	Nalepa and Quigley (1980)
Hirudinea	W(μg) = 721.6	Nalepa and Quigley (1980)
Parasite (Cestode)	W(mg) = .1	✹
Fish Egg -- lake herring -- sculpin	W(g) = .0012747 W(g) = .0022614	✹
Fish (Sculpin) (Alewife) (Bloater) (Smelt)	log W(g) = -4.02 + 2.45 log L(mm) $W(g) = 57.049E\text{-}6\ TL^{2.2767}$ $W(g) = 61.253E\text{-}9\ TL^{3.6696}$ $W(g) = 49.624E\text{-}9\ TL^{3.6297}$	Mohr (1984) Elliot et al. (1996)

Plant Seeds	W(mg) = .009	✷
Gravel	W(mg) = 2.7	✷

Of course log is log base 10 and ln is natural log

* L should be multiplied by .90 (approx.) because of measurement differences.

** L is $\log_{10}$ length and W is $\log_{10}$ weight

*** Conversions of similar taxa were used as none could be found in the literature for taxon indicated. Conversions used were as follows: *Ophryoxus (D. galeata), Macrocyclops (Mesocyclops), Daphnia longiremis (Daphnia retrocurva), Senecella (Limnocalanus), Leptodiaptomus ashlandi (Leptodiaptomus minutus)*, Bryozoa Floatoblast (Tardigrada)

@ Probably wet weight so I'll use the Mytilus edulis wet weight-dry weight relationship found in Sprung in the Zebra Mussel biology book

λ First value is for summer *Bythotrephes* in Lake Erie and the second is for Lake Superior *Bythotrephes* in the fall. SL stands for Spine Length. TL stands for total length and was from Lake Ontario in fall.

✷ Items we weighed ourselves

REFERENCES:

Culver, D. A., M. M. Boucherle, D. J. Bean, and J. W. Fletcher. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. Can. J. Fish Aquat. Sci. 42:1380-1390.

Conway, J. B. 1977. Seasonal and depth distribution of *Limnocalanus macrurus* at a site on western Lake Superior. J. Great Lakes Res. 3(1-2):15-19.

Dumont, H. J., I. Van de Velde, S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia(Berl.) 19:75-97.

Eaton, K. A. 1983. The life history and production of *Chaoborus punctipennis* (Diptera: Chaoboridae) in Lake Norman, U.S.A. Hydrobiol. 106:247-252.

Edmondson, W. T. 1955. The seasonal life history of *Daphnia* in an arctic lake. Ecol. 36(3):439-455.

Elliot, R. F., P. J. Peeters, M. P. Ebener, R.W. Rybicki, P. J. Schneeberger, R. J. Hess, J. T. Francis, G.W. Eck, C. P. Madenjian. 1996. Conducting diet studies of Lake Michigan piscivores -- a protocol.

Lake Michigan Technical Committee Report No. 96-2. U.S. Fish and Wildlife Service, Green Bay Fisheries Resources Office, Green Bay, WI.

Garton, D. W., and D. J. Berg. 1990. Occurrence of *Bythotrephes cederstroemi* (Schoedler 1877) in Lake Superior, with evidence of demographic variation within the Great Lakes. J. Great Lakes Res. 16:148-152.

Garton, D. W., D. J. Berg, and R. J. Fletcher. 1990. Thermal tolerances of the predatory cladocerans *Bythotrephes cederstroemi* and *Leptodora kindtii*: relationship to seasonal abundance in western Lake Erie. Can. J. Fish. Aquat. Sci. 47:731-738.

Hart, R. C. 1987. Population dynamics and production of five crustacean zooplankters in subtropical Lake le Roux, South Africa. Freshw. Biol. 18:287-318.

Hawkins, B. E., and M. S. Evans. 1979. Seasonal cycles of zooplankton biomass in southeastern Lake Michigan. J. Great Lakes Res. 5:256-263.

Makarewicz, J. C., and H. D. Jones. 1990. Occurrence of *Bythotrephes cederstroemi* in Lake Ontario offshore waters. J. Great Lakes Res. 16(1):143-147.

Meyer, E. 1989. The relationship between body length parameters and dry mass in running water invertebrates. Arch. Hydrobiol. 117:191-203.

Mohr, L. C. 1984. The general ecology of the slimy sculpin (*Cottus cognatus*) in Lake 302 of the Experimental Lakes Area, northwestern Ontario. Can. Tech. Rep. Fish. Aquat. Sci. No. 1227, pp 20.

Nalepa, T. F., and M. A. Quigley. 1980. The macro- and meiobenthos of southeastern Lake Michigan near the mouth of the Grand River, 1976-77. NOAA data report ERL GLERL-17 Great Lakes Environmental Research Laboratory, Ann Arbor, MI.

Rogers, L. E., W. T. Hinds, and R. L. Buschbom. 1976. A general weight vs. length relationship for insects. Ann. Ent. Soc. Am. 6:387-389.

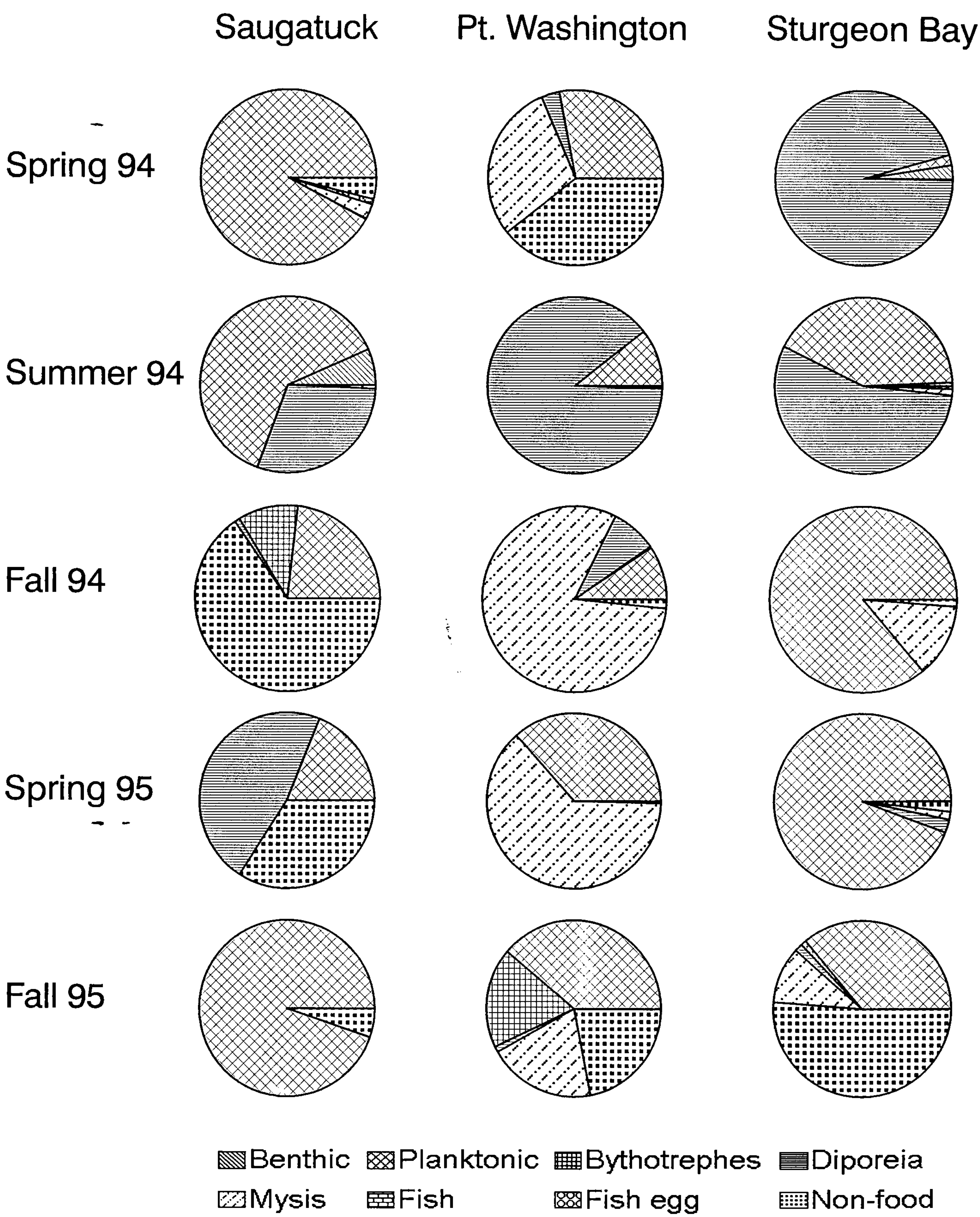
Rosen, R. R. 1981. Length-dry weight relationships of some freshwater zooplankton. J. Freshw. Ecol. 1:225-229.

Shea, M. A., and J. C. Makarewicz. 1989. Production, biomass, and trophic interactions of *Mysis relicta* in Lake Ontario. J. Great Lakes Res. 15:223-232.

Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. Freshw. Biol. 10:375-383.

Sprung, M. 1993. The other life: an account of present knowledge of the larval phase of *Dreissena polymorpha.* In *Zebra Mussels: Biology, Impacts, and Control,* T. Nalepa and D. Schloesser, Eds., Lewis Publishers, Ann Arbor, MI. pp 39-53.

Winnell, M. H., and D. S. White 1984. Ecology of shallow and deep water populations of *Pontoporeia hoyi* (Smith)(Amphipoda) in Lake Michigan. Freshwat. Invertebr. Biol. 3(3):118-138.



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Planktonic
Bythotrephes
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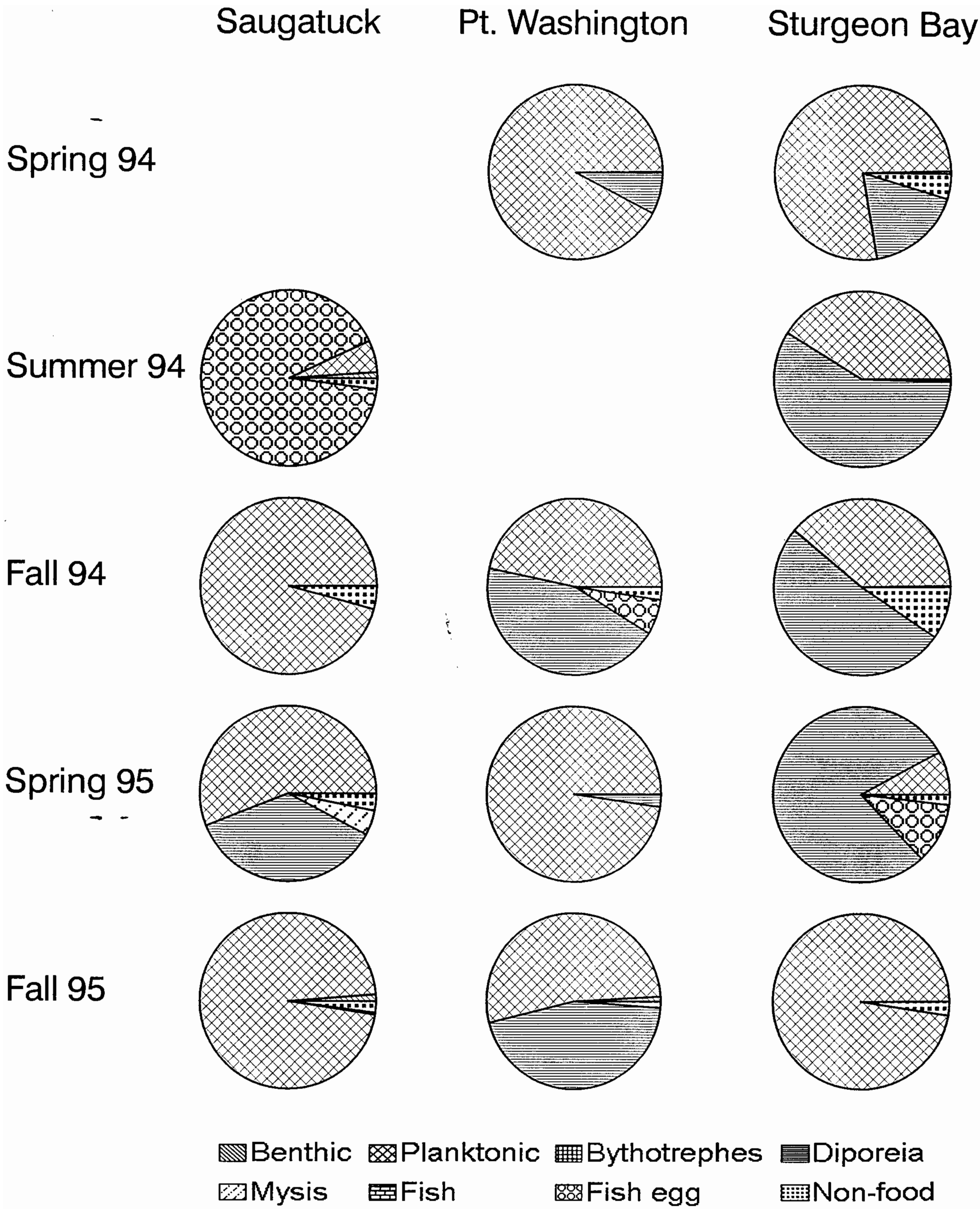
Mysis
Fish
Fish egg
Non-food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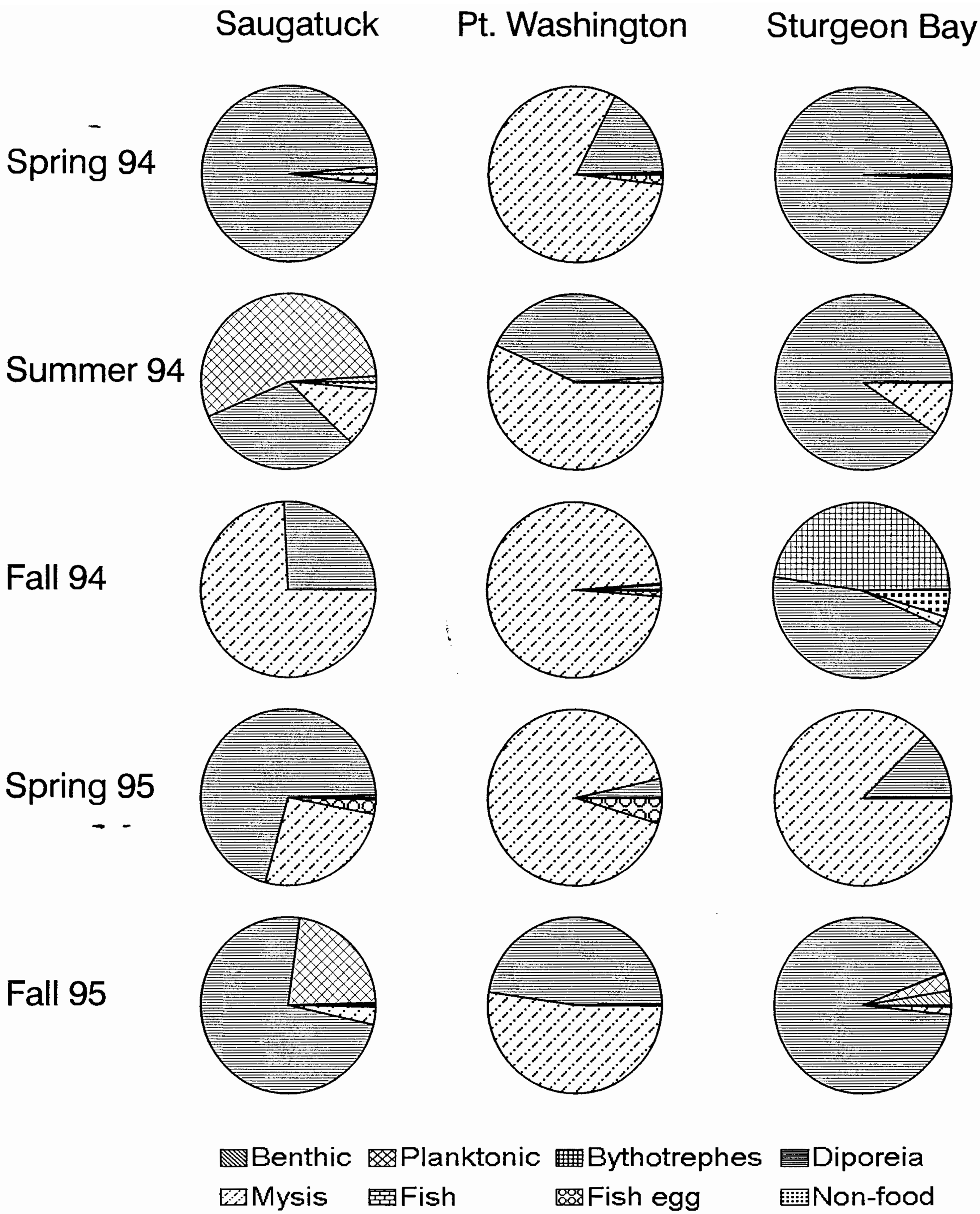

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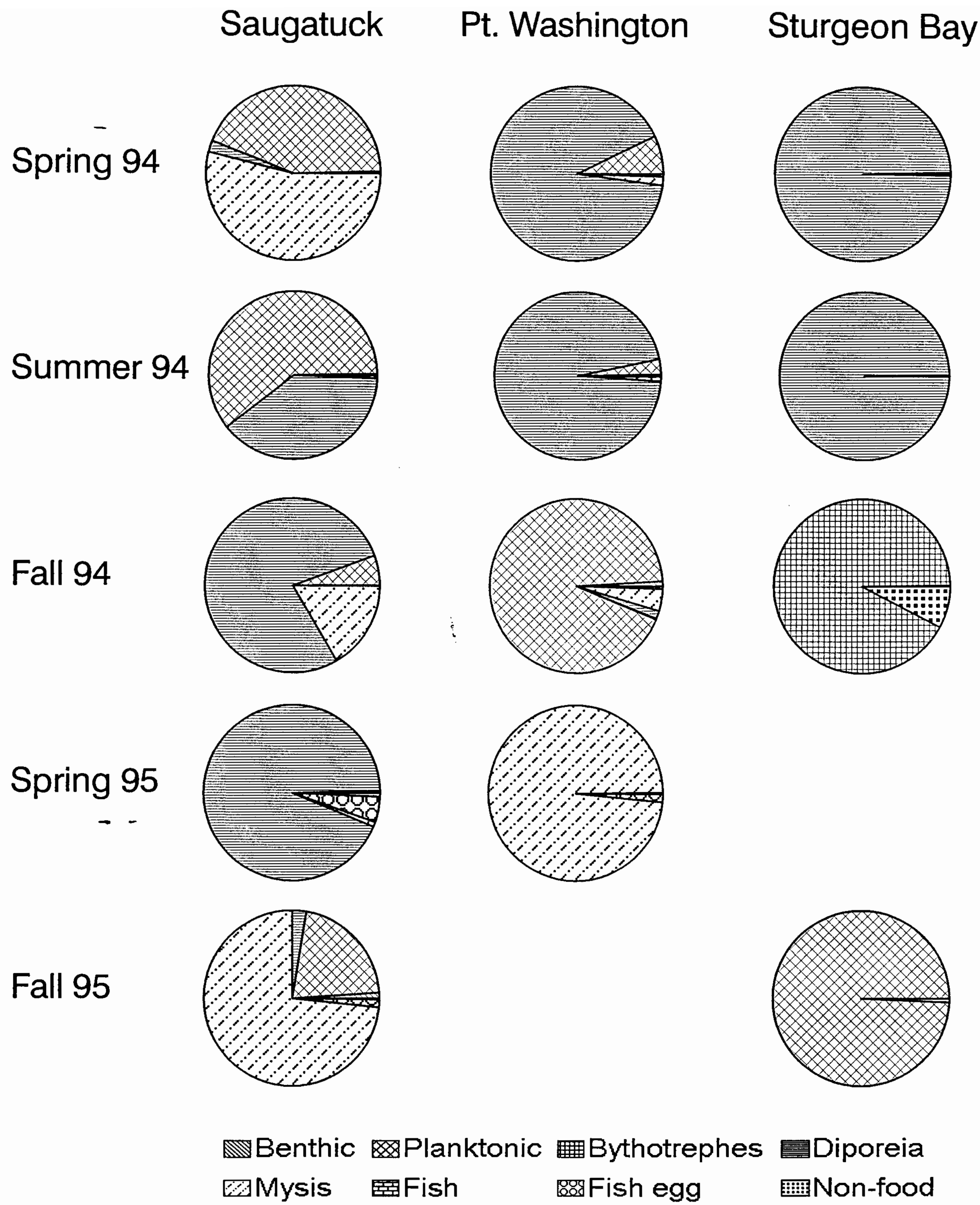

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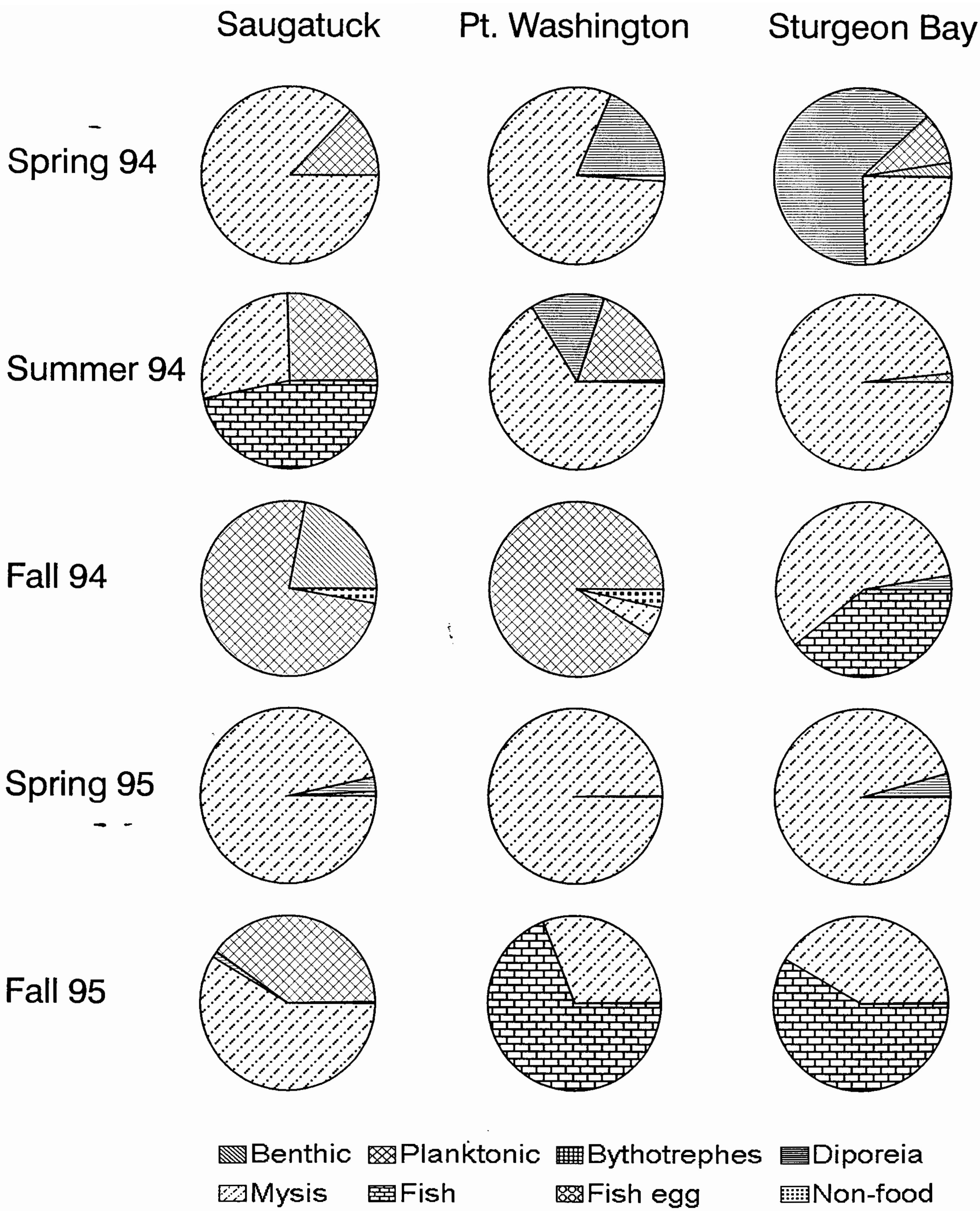
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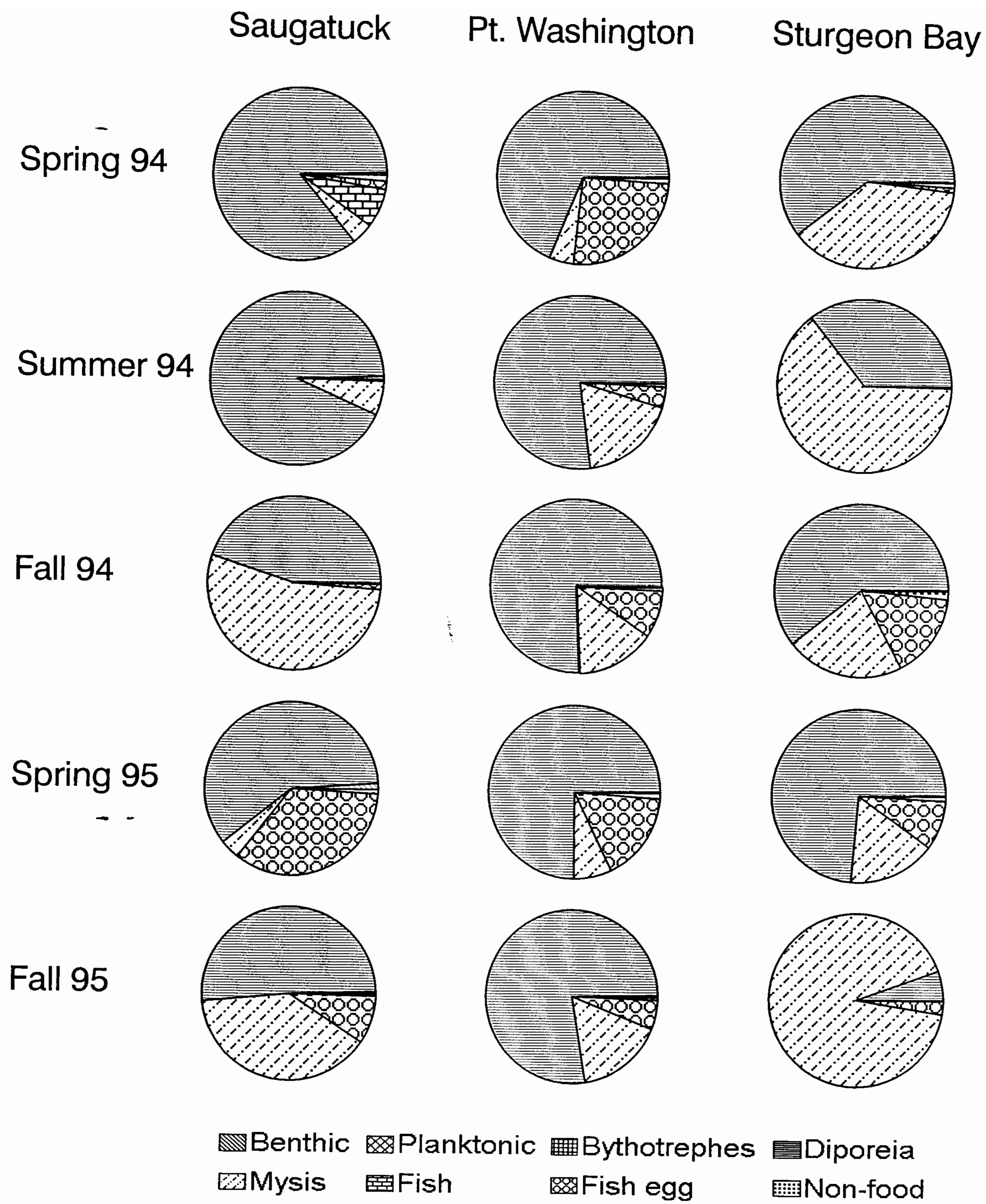
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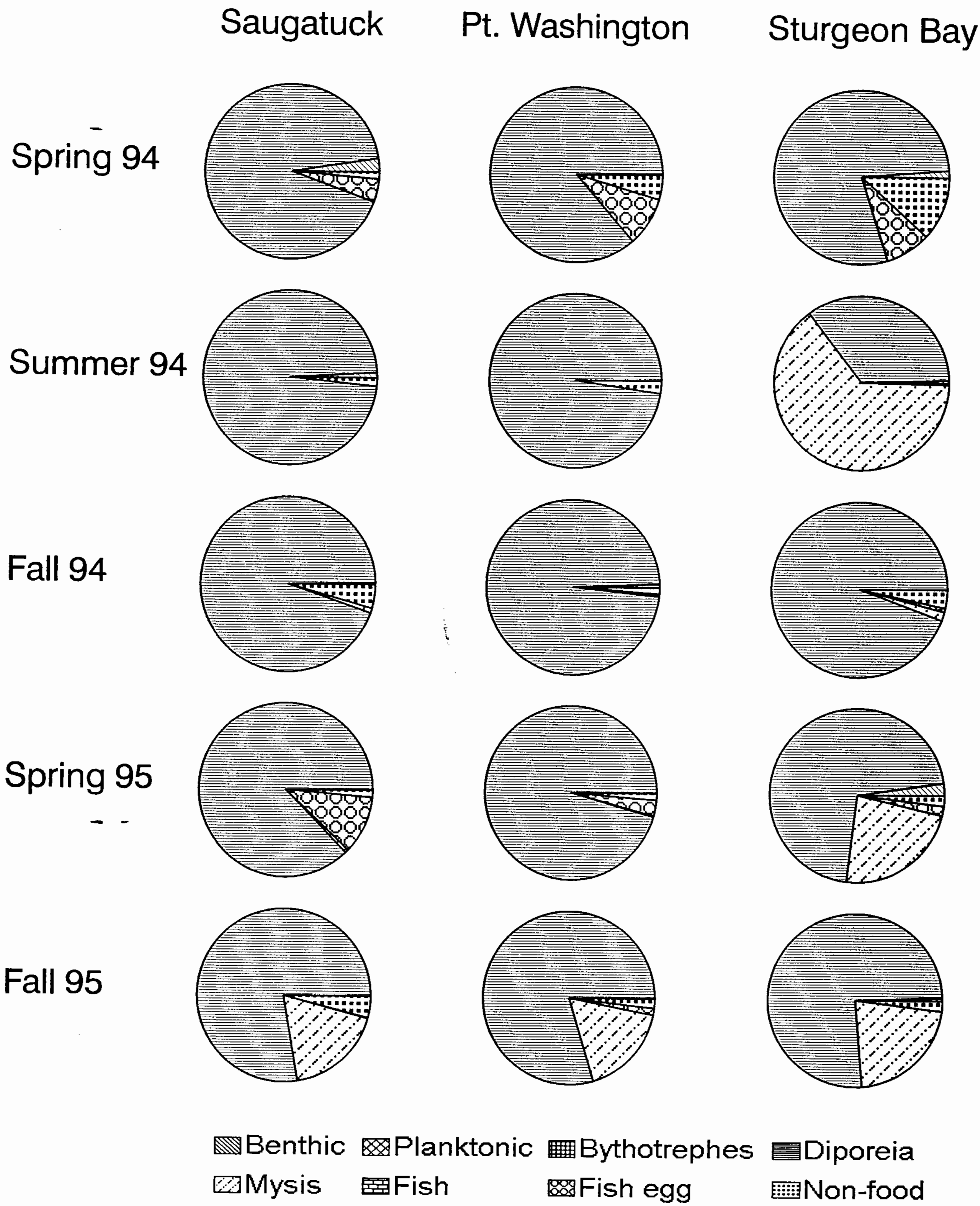

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